

Toward a Reconstructive Understanding of Behavior: A Response to Reese

Daniel Bullock
Boston University

I agree with Reese's (1996) conclusions about the debt of neurobiology to behavior analysis. As Von Frisch put it, "Nothing in neurobiology makes sense, except in the light of behavior." But I disagree with Reese's conclusions about the relevance of neurobiology to psychology, and therefore to behavior analysis. At issue are both the historical task of psychological science and the research tactics that psychologists can fruitfully choose in 1996.

At the birth of modern experimental psychology, there was little systematic information about the robust behavioral characteristics of animals. There was also little information about the nature of the physical systems—the neural systems—that are most responsible for the radically different behavioral characteristics observable across animal phyla and species. There was no hope of explaining even the few well-characterized behavioral characteristics as causal consequences of a well-understood set of mechanisms working together in a specified environment. Thus, one of the best paths to understanding other kinds of natural behavior, namely as emerging from the interactions of physical mechanisms within physical contexts, was practically unavailable. It therefore made sense to adopt a more abstract perspective vis-à-vis animal behavior, and to focus on the autonomous task of precisely describing behavioral characteristics, especially functional relations.

The cost of this abstract tack was temporary disconnection from understanding by rigorous imaginative reconstruction via mathematical modeling of interactions among neurobiological mechanisms and other contributing factors. Thus, there was also a disconnection from applications—such as how to repair breakdowns or how to build stable, intelligent machines—that require the deeper understanding that comes from imaginatively reconstructing a studied natural system with the aid of a dynamic model.

Unlike Reese, I believe that the situation responsible for the "disconnection" at the birth of modern psychology no longer exists. For many behavioral characteristics, it is now practical to conduct rigorous research on how they emerge as causal consequences of sets of brain mechanisms operating in context. For that reason, I cannot agree with Reese's conclusion that behavior analysis "will not suffer if behavior analysts ignore physiological processes" (p. 61). His conclusion rests on a misreading of the state of neurobiology, but also on overly restrictive views of both the natural scope of physiology and the place of behavior analysis in modern science.

First, the fact that behavior analysts who are ignorant of neurobiology can make further progress by discovering and documenting additional behavioral characteristics of animals is no argument against the relevance of an understanding of neurobiological mechanisms to behavior analysis. There now exists a huge set of results of behavior analyses, within which we may include the behavioral characteristics documented by a hundred years of research in cognitive psychology, social psy-

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Address correspondence to Daniel Bullock, Cognitive and Neural Systems Department, Boston University, Boston, Massachusetts 02215.

chology, perceptuo-motor psychophysics, and ethology. This set allows us to pose and pursue an answer to the question: What relatively small set of neurobiological mechanisms can—in the combinations sampled by distinctive species, and when embedded in life contexts—generate the enormous set of behavioral characteristics? If we can answer this question, then we will have answered the questions about human nature (such as, what about human nature makes us capable of generating such a wide range of behaviors, typically well-adapted behaviors that are often assembled with startling rapidity?) that attracted many of us to psychology.

On the other hand, if we could not answer such questions, then psychology would remain a loose collection of rules of thumb, of demonstrations of “effects,” and of many alternative ideologies, each with its own theories of how more complex behavioral phenomena are derived from simpler phenomena. The reason that neurobiological methods alone cannot formulate correct theories was well stated by Von Frisch (quoted above). The reason that behavior-analytic methods alone are also insufficient for characterizing the physical bases of human behavioral characteristics is that it is often impossible to choose, from among the many functionally equivalent alternatives possible in principle, just that complex of mechanisms that is actually being used. Indeed, if the set of alternatives were truly proposed with no guidance from neurobiological data, it is unthinkable that any of the alternatives would be correct. Although we may use this as a basis for criticizing free-floating cognitive theories, it is no basis for eschewing physically grounded theories. To make it such would be to retard psychology’s movement toward the kind of grand syntheses exemplified by modern genetics and embryology.

A concrete example shows the practicality of rigorously studying how interactions among small sets of neuro-

biological mechanisms can explain behavioral characteristics. In Reese’s survey of neurobiology, he gives a prominent place to a paper by Thompson (1986), which reported the state of the art, in 1986, of attempts to discover the neurobiological mechanisms responsible for the classically conditioned nictitating membrane response (NMR) in rabbits. A torrent of relevant research in the decade since 1986 has validated many aspects of Thompson’s circuit model, and for 6 years my colleagues and I have been conducting computer simulation studies based on a set of mathematical models of various updated versions of the circuit, with a focus on the cerebellum. The cerebellum was firmly established as a critical element in adaptive timing of conditioned NMRs in experiments by Steinmetz (1990), who showed that direct stimulation of two classes of fibers that converge on cerebellar Purkinje cells, namely parallel fibers and climbing fibers, could, for purposes of learning with the correct interstimulus interval, serve as substitutes, respectively, for externally presented conditioned (CS) and unconditioned (US) stimuli. In addition, tremendous strides have been made in the last 5 years regarding Purkinje cell biophysics. Based on these neurobiological results and a wide range of behavioral experimental results, we (Bullock, Fiala, & Grossberg, 1994; Fiala, Grossberg, & Bullock, 1995) have shown that a metaphysically gapless, physical explanation can be given of adaptive timing properties of the molar behavior—trial-by-trial changes in the timing and topography of the conditioned NMR—in terms of a neural macrocircuit whose function as an adaptive timing circuit critically depends on details of an intracellular biochemical cascade now known to exist in Purkinje cells. In particular, the model shows how glutamate released by parallel fibers (and indicating CS onset) can have both immediate and delayed effects on Purkinje cells through ionotropic and metabotropic channels, respectively. The

delayed effects mediated by the metabotropic channels give ensembles of Purkinje cells the competence to detect correlations between CS events and the US events that may occur seconds later, as required for learning to produce a conditioned response timed to begin just before the expected onset of the US. This mechanistic, neural-network explanation comes in the form of a mathematical (differential equation) model capable of making detailed predictions regarding the way that behavior and learning evolve through time. Learning (definable here as a normally adaptive, experience-dependent physical modification of the neural system) occurs through protein phosphorylation of both the ionotropic (AMPA) channel and a calcium-dependent potassium conductance. This new model shows how known processes, studied separately by many different neurobiologists, can interact to serve adaptive timing. Though it awaits experimental test, the model can be seen as a further elaboration of the well-supported circuit model of Thompson (1986). But the key fact is that many such psychological (molar behavior explaining!) models are showing steady growth in scope, and can be formulated with such detail, thanks to the huge databases on neurobiological mechanisms and behavioral characteristics.

Our treatment has the elements promised above: We show that a wide range of behavioral characteristics that have been reported in different conditioning studies can be seen as "signatures" of a circuit that includes the cerebellum as a critical element. Because the same basic cerebellar circuit has been implicated in many varieties of motor learning not usually treated as examples of classical conditioning, the common mechanism allows linkage of a very large set of behavioral operating characteristics not previously linked on behavioral grounds alone. Also, the explanation is not "reductionist" in any meaningful sense. In a "neural dynamics" account, the physical context and the action-perception cycles that it

makes feasible are key to the experience-dependent morphogenesis of the neural network, and therefore of behavior. Neither the global behavioral characteristics nor the behaviors themselves are claimed to be preformed in any of the neural mechanisms as such (see Bullock, 1987, for more on non-reductionist explanations of intelligent behavior). In fact, it becomes clear from studying behaviors as literally "net cellular effects" that all instances of the kinds of behavior that are focal for behavior analysts are creative assemblages (as Chomsky once argued, but with an unnecessary restriction to complex verbal behavior).

Conclusion

A grand synthesis of neurobiology and behavior analysis (including cognitive psychology, social psychology, and psychophysics) is well underway. Within the span of the research careers of today's scientists, we will have precise mechanistic explanations of a very large set of normal and abnormal behavioral characteristics within a unified theoretical framework (i.e., with a much smaller number of fundamental mechanisms than of behavioral characteristics explained). This synthesis should eliminate the last vestiges of metaphysical dualism (e.g., the covert dualism in the claim that behavior and physiology are corresponding events in separate universes of discourse). Our growing experience at fusing neurobiology and psychology will take us from seeing double to seeing one thing, in vibrant depth.

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